MALACOLOGIA, 2011, 54(1–2): 109–118

GENDER-BASED DIFFERENCES IN FLORIDA APPLE SNAIL (*POMACEA PALUDOSA*) MOVEMENTS

Patricia L. Valentine-Darby[1], Philip C. Darby[2]* & H. Franklin Percival[3]

ABSTRACT

Gastropod movements have been studied in the context of habitat selection, finding food and mates, and avoiding predation. Many of these studies were conducted in the laboratory, where constraints on spatial scale influence behavior. We conducted a field study of Florida apple snail (*Pomacea paludosa*) movements using telemetry. We hypothesized that Florida apple snail movements were driven by reproductive activity, and that gender differences would be evident. We documented male and female directions and distances traveled. We also conducted a trapping study that included conspecific bait to test if the presence of females attracted more males as measured by M:F ratios in traps. The greatest distances traveled were by males, and males were more likely to maintain a consistent bearing compared to females. Male distances peaked in what typically corresponds to peak breeding season. M:F ratios in traps were positively associated with reproductive activity in the study population as measured by egg cluster counts. Conspecific bait had no effect on the number of males or females captured. However, if a female crawled into the trap, we observed greater numbers of males compared to those with no trapped females. Males may have tracked females to increase mating encounters, following slime trails, as seen in other aquatic (including other *Pomacea*) snails. The capacity for mate finding has implications for reproductive success in the relatively low density populations often seen for *Pomacea paludosa*.

Key words: *Pomacea paludosa*, reproduction, movements, Florida, apple snail.

INTRODUCTION

A gastropod's capacity for movement directly affects its ability to find suitable habitat in heterogeneous environments (Coffin et al., 2008), food (Snider & Gilliam, 2008), and mates (Erlandsson & Kostylev, 1995), and to avoid predation (Dickey & McCarthy, 2007) (also reviewed by Croll, 1983). Although many environmental factors affect the direction and distance traveled by snails (e.g., currents and benthic habitat structure, as described in Hoffman et al., 2006), chemoreception appears to be the principle mode by which many snail species' movements are directed (Croll, 1983). Snails may respond to chemicals in the trails of other snails, or to air-borne (for terrestrial snails) or water-borne chemical gradients of food, predators, or other snails (Dinter, 1974; Takeda & Tsuruoka, 1979; Croll, 1983; Shaheen et al., 2005). Much of the research on aquatic snail movements reflects laboratory studies at relatively small spatial scales, compared to the natural environments across which snails traverse. The Florida apple snail (*Pomacea paludosa* Say) (Gastropoda: Ampullariidae) is the largest native freshwater snail in North America (Pennack, 2001), with a range restricted primarily to the lakes and wetlands of peninsular Florida (Thompson, 1984). Darby et al. (2002) reported average weekly distances traveled by Florida apple snails as 15 m/wk. This led to questions about what drives apple snail movements under natural conditions. Apple snails did not move along gradients of temperature, dissolved oxygen, or water depth (to avoid being stranded in a drying marsh) during a March–June field study in Florida (Darby et al., 2002). Apple snails did move among a wide range of habitat types, including sawgrass (*Cladium jamaicense* Crantz), cattail (*Typha* spp.), and wet prairie (dominated by low profile grasses and sedges), as indicated

[1] The Pomacea Project, 1765 East Nine Mile Road, Suite 1, #369, Pensacola, Florida 32514, U.S.A.
[2] Department of Biology, University of West Florida, 11000 University Parkway, Pensacola, Florida 32514, U.S.A.
[3] Florida Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, University of Florida, Gainesville, Florida 32611, U.S.A.
*Corresponding author: pdarby@uwf.edu

by telemetry and mark-recapture studies (Darby et al., 2002; Valentine-Darby et al., 2008). Peak apple snail egg cluster production most often occurs in April–May (Darby et al., 2008), so movement patterns during this time of year may be associated with reproduction. In lieu of environmental factors being the primary driver of the magnitude and direction of snail movements, at least during spring and summer, we hypothesized that Florida apple snail movements vary as a function of gender and changes in their reproductive status as seen in other aquatic snails (Pardo & Johnson, 2004).

Apple snails are dioecious (Aldridge, 1983). Females must find suitable structure for above-water egg cluster deposition (i.e., oviposition), typically emergent plant stems with diameters > 6 mm (Turner, 1996). Florida apple snails often occur at densities < 0.2 snails/m^2 (Darby et al., 2006), so their ability to track down potential mates may be especially critical for recruitment in many central and south Florida wetlands. Hanning (1979, p. 45) stated that "Females are searched for by the males ..."; he referred to both laboratory and field observations, but provided no information on how he came to this conclusion. A recent laboratory study of *Pomacea canaliculata* found that both males and females followed mucous trails of snails of the opposite sex (Takeichi et al., 2007); males were also attracted to water conditioned with females, suggesting an attraction to one or more water-borne sex pheromones.

We used a combination of telemetry and trapping studies to examine whether variation in distance and movement patterns of Florida apple snails in the field was associated with gender and/or reproductive activity. We hypothesized that snail movement rates were positively associated with reproductive activity (as indicated by egg cluster counts). We also hypothesized that males and females would exhibit different patterns of movement over space and time, in part because of earlier suggestions that males track down females (as noted above), and because females must target microhabitat patches that support oviposition.

METHODS

Study Area and Sampling Periods

Our study site was in the eastern-most portion of the Blue Cypress Water Management Area (BCWMA), part of the Upper St. Johns River Basin, in Indian River County, Florida. Details of the study site, including a map, were published in Darby et al. (2002). The plant community in this area consisted of a mosaic of sawgrass patches surrounded by emergent macrophytes (primarily *Eleocharis cellulosa* and *Panicum hemitomon*) and scattered areas of open water (Lowe, 1983; Darby et al., 2002). The telemetry study was conducted March–July, 1995, and the wire funnel trap study was conducted February–August, 1996. Both studies included the seasonal initiation, April–May peak, and subsequent decline of snail egg production, as described in Darby et al. (2008). We studied the same BCWMA snails in 1995 that were the subject of Darby et al. (2002) and Darby et al. (2003). We used an airboat to access the study site, but all visual searches, tracking of snail movements, and trap checks were conducted on foot.

Telemetry Study

We used miniature radio-transmitters (1.6 gram) to track snail movements. Details on transmitter attachment and monitoring were described in Darby et al. (2002). Adult apple snails (n = 47) were collected using visual searches and wire funnel traps. Visual searches consisted of collecting female snails nearing their completion of egg-laying at night, and from daytime searches for snails in clear water. Twenty-four snails were sexed based on shell morphology (Hanning, 1979), seven females were identified while laying eggs, and 16 snails were found mating (in some cases with a snail already bearing a transmitter). Copulating pairs were gently pulled apart; males were identified by their penis sheath (Hanning, 1979; also see Andrews (1964), and Albrecht et al. (1996) for observations of *P. canaliculata*). We noted that egg-laying females and mating males had the characteristic shell morphology by which we identified gender for the aforementioned 24 snails.

Hanning (1979) estimated that sexual maturity for *P. paludosa* was ≥ 30 mm shell length, so snails exceeding this length were assumed to be sexually active in our study. We placed transmitters on 25 females (shell lengths 36 to 53 mm) and on 22 males (36 to 46 mm). The transmitters were attached to the outside of the snail shell using the minimum amount of marine epoxy required for a firm hold. Snails with transmitters were returned to their original location within 20 minutes of capture. Snails were released throughout the study period in a staggered entry design to replace dead snails or transmitters with dead batteries (details in Darby et al., 2002).

We used standard telemetry equipment to locate radio-bearing snails within a 2 to 3 m diameter circle. Magnet-induced signal alteration (Darby, 1999) was used to pinpoint each snail location. On every monitoring occasion, each snail was picked up to confirm that it was alive and then returned to its exact location. Snail locations were marked with polyvinylchloride (PVC) poles driven into the substrate, and we wrote the radio-frequency of each snail on its PVC marker.

Distances traveled (n = 81) were documented at weekly intervals until the snail or the transmitter battery died. Movements starting from initial capture locations were excluded from analyses, because of the disturbance caused by snail handling and transmitter attachment. We also excluded locations of snails found dead. Each time a snail was located, the straight-line distance between its current location and its last-monitored location was recorded. A compass was used to measure the direction the snail had moved from its previous location. Other metrics measured at each location during the telemetry study (e.g., temperature, dissolved oxygen, depth) have been reported in Darby et al. (2002).

Telemetry Data Analyses

We have already reported the effects of environmental metrics (depth, temperature, oxygen) on the movements of the 47 snails with transmitters discussed herein, and no significant trends were found (Darby et al., 2002). Water temperatures during the study, all measured between 11:30 and 13:00 hrs, averaged (± SD) 28.8 ± 3.3°C. When temperatures fall below approximately 20–21°C, apple snail movements decline significantly (Stevens et al., 2002), but temperatures never fell below 23°C in our radio-telemetry study. Only snail movements in water ≥ 10 cm deep were included in our analyses, because in shallower depths snails stop moving (Darby et al., 2002).

We used a mixed model ANOVA (snails monitored = random effect; gender and week monitored = fixed effects) for all analyses of snail distances traveled. The analysis produces F-statistics that are not a ratio of sums of squares, but are instead from a Wald-test (Searle et al., 1992). Distances traveled (m) were transformed using the function $\log_{10}$ (m +1) in order to meet assumptions of ANOVA.

We tested for the effects of gender, biweekly interval (e.g., March 1–14; March 15–28), and their interaction, on the weekly distances traveled. We grouped weekly data into biweekly intervals (BWI) to increase our sample size; due to deaths and battery failure, we often had ≤ 2 individuals to monitor in a given week. We increased our sample size to 4–6 (the number of different individuals for which we documented movements) by analyzing data as a function of BWI. If an individual snail's movements were measured twice within a BWI, the mean value for the 7-d distances traveled was used for that individual for that BWI. We performed repeated measures ANOVA (Crowder & Hand, 1990; SAS, 1992) to account for repeated measure of individual transmitter-bearing snails over two or more BWIs. We further explored the gender*BWI interaction using the SLICE procedure in SAS; that is, we partitioned the interaction effect to distinguish between variation in female versus male movements over time (SAS, 1992).

We constructed patterns of movement (distances and directions) for snails (n = 11) that were monitored on three or more occasions. We used Watson's two-sample test (U^2) (Jammalamadaka & Sengupta, 2001) to analyze the turning angles (i.e., the angle created by the intersection of two consecutive movement vectors) to see if the two sets of angular data (male and female) had the same distributions. Critical values for the test statistic and associated P-values for small sample sizes were obtained from Mardia (1972). We also tested if there was a gender difference for maintaining a bearing (degrees from north) over several consecutive movements using a Raleigh test (*R*) (Jammalamadaka & Sengupta, 2001). The specific direction to test for each snail was determined by the compass direction created by the line that intersected the start and end point from a series of movements.

Trapping Study

Wire funnel traps are a form of passive trapping that requires snails to move into the traps. We used a modified version of a commercially available crayfish trap; for details, see Darby et al. (2001). Pilot studies of funnel trap protocols led us to two important points regarding the use of these traps. First, bait was not needed to attract snails to the traps (Darby et al., 2001); snails entered the traps during horizontal movements and/or vertical ascents to breathe air. Second, sex ratios of captured snails suggested that males may have followed females into the traps; whenever we found a female, one to six males were also in the trap.

We hypothesized that as reproductive activity increased (as measured by egg production; see below), the male to female ratio (M:F) of captured snails in the traps would increase. Hurdle (1974) and Hanning (1979) observed that individual females mate frequently, with multiple males, throughout the egg-laying season. Andrews (1964) described multiple males attempting to mate with individual *Pomacea* females. Females lay egg cluster masses at an average rate of approximately one cluster each one to two weeks (at times producing up to three a week) for up to several months (Hurdle, 1974; Hanning, 1979). Therefore, egg laying activity should track mating activity, and increased male efforts to find mates should result in increased M:F ratios in traps. Our hypothesis regarding increased M:F ratios was based in part on Hanning's (1979) report of males tracking females. Hanning also reported a breeding season (January–June) sex ratio of 1:1 for *P. paludosa* in Florida (Lake Okeechobee), with an overall ratio, based on 868 snails collected over 1.5 years of monthly samples, of 1 female to 0.75 males. Population sex ratios of approximately 1:1 have been reported in other *Pomacea* species (Yusa & Suzuki, 2002; Cowie, 2002). Consequently, deviation from a 1:1 ratio in passive traps reflects differences in male versus female capture rates. [Funnel traps do not randomly sample the population as indicated by highly skewed M:F ratios observed in our pilot study. Randomly sampling our study population to obtain the population sex ratio, for example, via throw traps, required considerable time and labor (Darby et al.,1999) beyond the scope of our resources at the time.]

We also tested whether or not baiting traps with live apple snails attracted snails, presumably via a water-borne pheromone. To hold the bait, we constructed an 8 cm-diameter cylindrical enclosure to set inside the funnel trap and permit the bait (snail) to reach the surface to breathe air. A cylindrical bait enclosure was installed in all traps. Approximately one-third of the traps were baited with adult females (F), one-third of the traps with adult males (M), and the remaining traps were not baited and served as controls (O). Traps were numbered, and the same type of bait was used in a given trap throughout the study.

We conducted six one-week trapping sessions from January 30–August 19. We initiated a trap session by placing 51 to 54 traps on PVC poles, approximately 5 m apart, throughout our study site. At the initiation of each of the six trapping sessions, traps were randomly distributed among the PVC poles to avoid any potential effect of trap location. Traps were placed in 20 to 60 cm of water from 1 to 10 m away from the ecotone created by sawgrass and mixed-emergent wet prairie habitats.

Traps were checked twice, at 3- to 4-day intervals, during each trapping session. Traps were not moved between checks. We measured the water temperature between 11:00 and 13:30 at each trap check. [The difference between surface temperatures and those near the substrate were consistently < 1°C apart, so we based our analyses on just surface temperatures.] During each trap check, the shells of at least 20 males and 20 females (randomly selected) were measured to ensure M:F ratios were based on adult-sized snails. Captured snails were released approximately 2 m from the trap.

Egg cluster production was monitored and used as an index of reproductive activity over time (e.g., Hanning, 1979; Darby et al., 2008). We sampled three transects during each session. A transect was a 30 m length of the outer edge of a sawgrass patch bordering our study sites, that is, we sampled the sawgrass-prairie ecotone (see Darby et al., 1999). Since we were primarily interested in the temporal pattern of egg cluster production, we sampled the same three transects, starting at the same point and moving in the same direction, at each monthly count. We deployed a 1 x 2.5 m PVC quadrat 12 times along each transect during each count.

Trap Data Analyses

We examined the effect of bait type (M, F or 0) using two separate analyses. First, we looked only at the number of males captured as a function of bait type (males= bait + session + session*bait). In the second, we looked at the number of females captured (females= bait + session + session*bait). The number of snails captured per trap (male or female) in each trap session was the total of both trap checks within each 7-d trapping session. Male or female snail counts were analyzed using a generalized linear models approach based on a Poisson distribution. The goodness-of-fit criterion indicated overdispersion, so we corrected for this using the pscale option in SAS (1992) based

TABLE 1. Results of mixed model ANOVA for snail distances traveled over the seven-day interval as related to biweekly interval (BWI), gender, and their interaction, and results of partitioning the gender*BWI effect (to distinguish between BWI effects for male and female 7-d distances) using the SLICE procedure in SAS (details in Methods).

Source	Numerator DF	Denominator DF	F Value	P-Value
GENDER	1	27	0.01	0.939
BWI	8	22	2.53	0.041
GENDER*BWI	7	22	2.10	0.086
female	8	22	1.39	0.257
male	7	22	3.64	0.009

on McCullagh & Nelder (1989). Male to female ratios were calculated for each trapping session. We excluded all trap checks with no snails and all traps that had no females (M:F for an individual trap would be undefined). [The effect of bait was ignored, see Results.] We tested the hypothesis that M:F ratios were positively correlated with egg cluster counts during the same period using Spearman's rank correlation analysis, and we report the average ratio and SE for each trap session based on ratios from individual traps. The sample size varied from 27 to 36 M:F ratios for each trap session. We also used the same approach to test the competing hypotheses that M:F ratio was associated with the linear progression of time (as trap session 1 through 6, representing February through August) or water temperature.

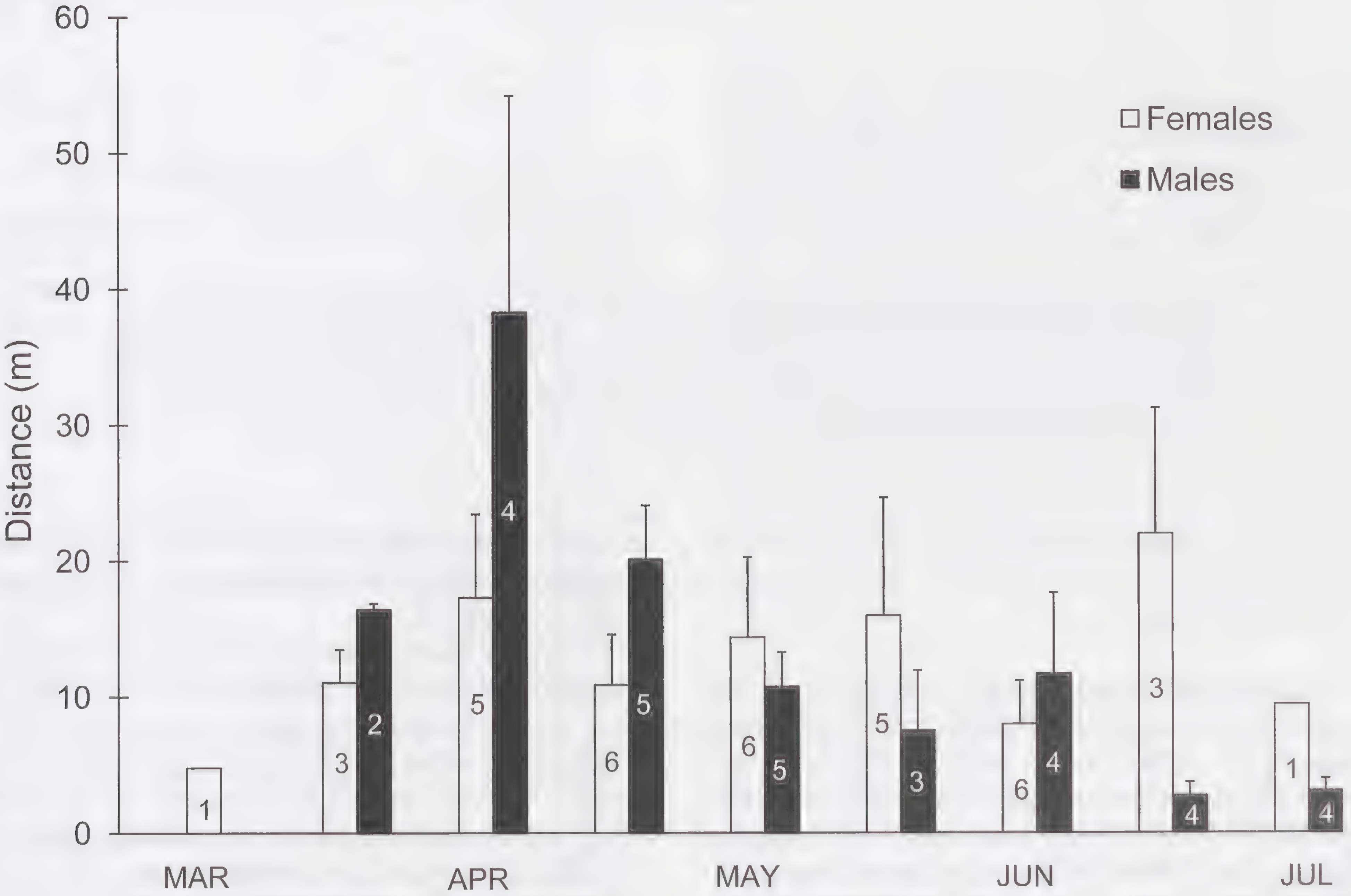

FIG. 1. Weekly distances traveled by male and female snails in BCWMA in 1995. Data are from snails in water depths > 10 cm. Error bars are standard errors. Sample sizes appear inside bars.

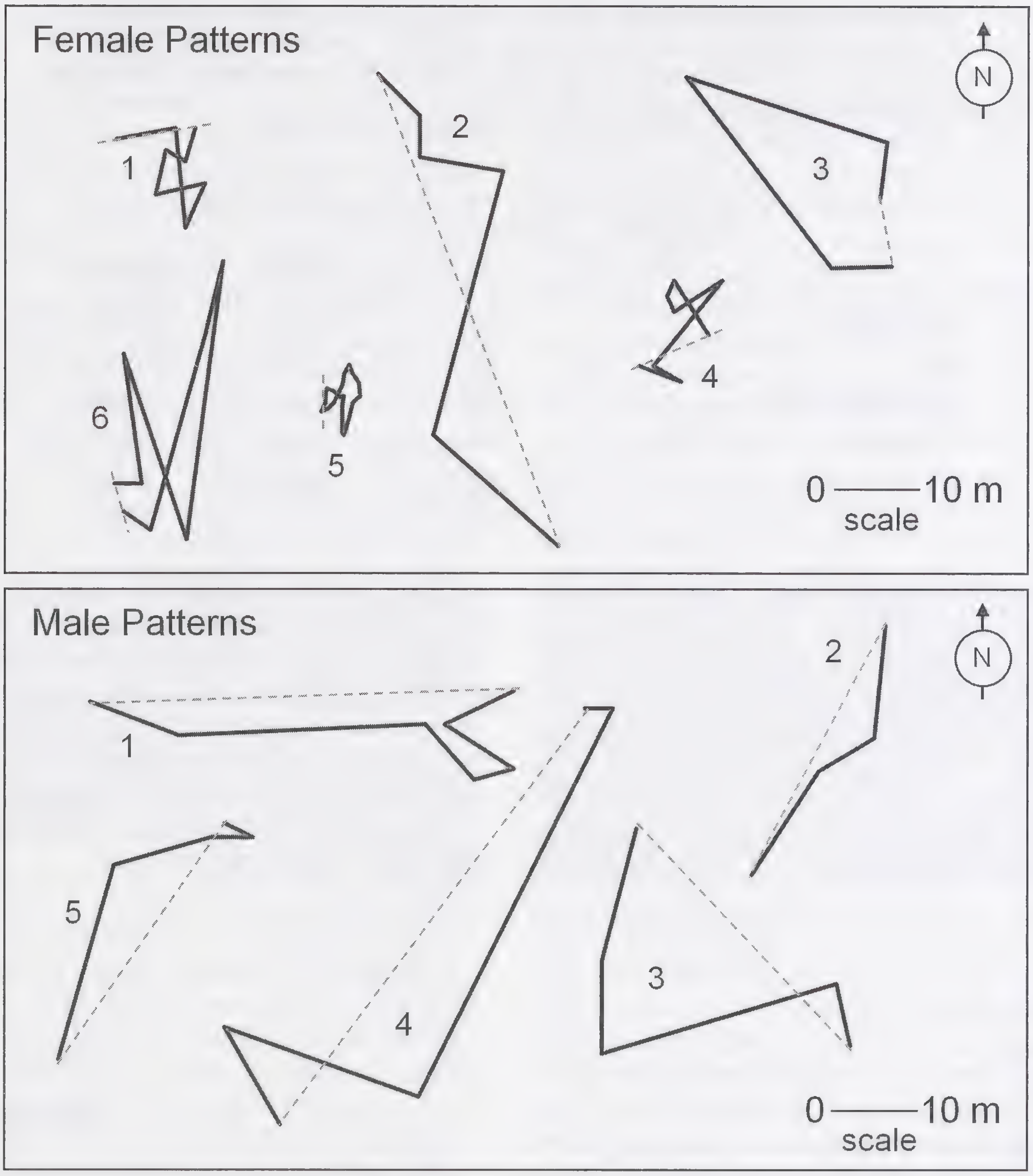

FIG. 2. Movement patterns (black solid lines) of six female (top panel) and five male snails (bottom panel) in BCWMA in 1995. Only snails for which three or more weekly movements were documented are included. Gray dashed lines intersect start and end points to show specific bearing for the Raleigh test for each snail. Vertical arrow indicates north (N). Patterns are to scale.

RESULTS

Telemetry Study

The overall average (±SD) weekly snail distance traveled was 14.8 ± 10.3 m. We found a significant difference in weekly distance traveled as a function of BWI over the 18 week period, but movement rates were not affected by gender (Table 1). However, when we partitioned the interaction effect to distinguish between male and female movements, we found no difference in distance traveled for females across BWI, but there was a significant difference for males (Table 1). Male average weekly distances varied over time with an April peak of 38 m (Fig. 1).

We found no difference in turning angles between males and females ($U^2 = 0.097$, $P > 0.1$). Five of six females did not maintain a specific bearing (Females 1, 3, 4, 5, 6, $R \leq 0.3$, $P \geq 0.14$; Female 2, $R = 0.82$, $P = 0.003$) (Fig. 2). In contrast, males were more likely to maintain a particular bearing (Males 1, 2, 3, $R \geq 0.6$, $P \leq 0.044$, Male 5, $R = 0.54$, $P = 0.066$, Male 4, $R = 0.26$, $P = 0.24$) (Fig. 2). All of these patterns included weekly movements during the April–May peak in reproduction.

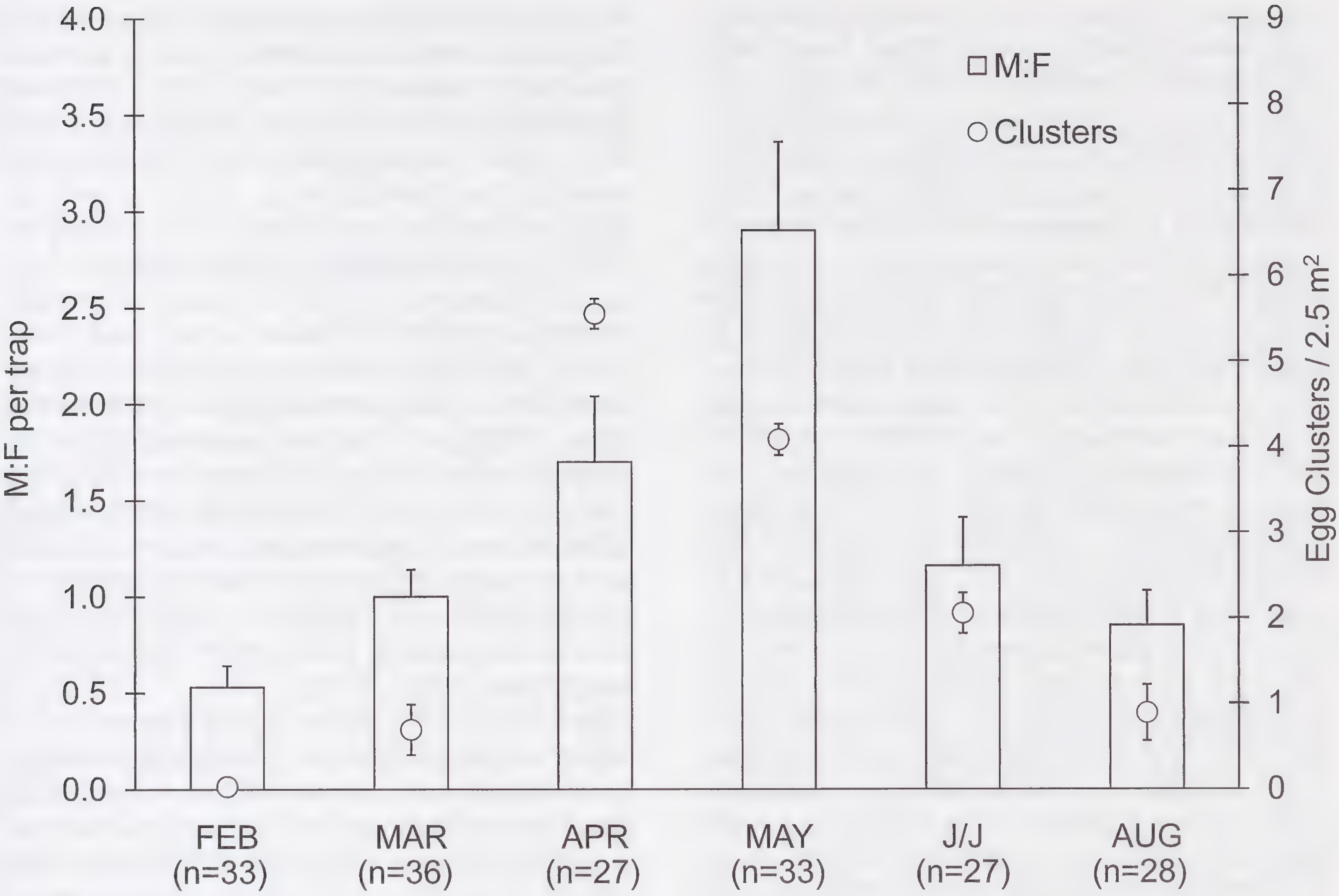

FIG. 3. M:F ratios per trap (bars) and egg clusters (circles) in BCWMA in 1996. Sample sizes in parentheses are for M:F ratios. Error bars are standard errors.

Trapping Study

A total of 846 snails were captured in the trapping study; 501 of these were males and 345 of these were females. Out of the snails randomly selected for shell measurements, female lengths were on average 38.6 ± 4.1 (SD) mm and males were 37.4 ± 3.1 mm.

Bait type (M, F, or O snail) did not affect the number of female snails or male snails captured ($\chi^2 = 1.86$, df = 2, P = 0.40 and $\chi^2 = 1.85$, df = 2, P = 0.40, respectively). There was a significant effect of trap session on the total number of females and males captured ($\chi^2 = 24.05$, df = 5, $P < 0.001$ and $\chi^2 = 130$, df = 5, $P < 0.001$, respectively). The average number of males per trap (±SD) was 0.88 ± 1.2 when no females were captured; if one or more females were in the trap, the average number of males was 2.1 ± 2.3. The M:F ratio of captured snails and egg cluster production varied over the seven month sampling period, peaking in April–May (Fig. 3). There was no linear relationship between the chronology of the trap sessions and M:F ratio ($\rho = 0.26$, P = 0.62), nor did water temperature (which was > 21°C except for February) affect the M:F ratio ($\rho = 0.52$, P = 0.29). There was a strong positive association between M:F and egg cluster counts ($\rho = 0.89$, P = 0.02). The three highest individual M:F trap ratios were 13:1 (n = 1), 8:1 (n = 1), and 6:1 (n = 3), all in April/May. We show data from only traps that had at least one F captured so we could show means and SE based on individual traps within a session (we cannot calculate a M:F ratio with zero females in the trap) (Fig. 3). However, if we look at total M:F ratio from all traps combined for each session (i.e., including traps with no females but some males), we see nearly identical M:F ratios and the same pattern (data not shown).

DISCUSSION

Florida apple snails routinely moved 15–20 m, and up to 83 m, a week. Although *Pomacea* snails can float (Burky & Burky, 1977; PCD pers. obs. in aquaria snails) and thereby potentially move with wind currents, in only one case did we observe a snail free floating during our tracking and trapping studies. We concluded that our movement data primarily represented crawling snails. When considering the distances moved, it should be noted that these distances represent a minimum distance traveled; apple snails, like other snails, unlikely move in straight lines (Tomiyama, 1992; Erlandsson & Kostylev, 1995). Like Pardo & Johnson (2004), we assumed that the weekly straight-line distances were proportional to the total non-linear distance actually traveled by snails. Although several studies of snail movements in laboratory and mesocosm studies have been conducted (e.g., Wells & Buckley, 1972; Hoffman et al., 2006), few exist for free-ranging freshwater snails. A similarly-sized freshwater snail, *Lavigeria coronata* (21–39 mm adults) moved 0.5 m/d, approximately 20 times their shell length per day (Michel et al., 2007). At 15–20 m per week (2.1–2.9 m/d), *P. paludosa* was moving approximately 50–70 times its shell length per day. Similar daily rates (2.8 m/d) were recorded for *Lanistes nyassanus* (Louda & McKaye, 1982), ampullarids similar in size to snails in our study population. Movement rates were noted for another apple snail (*Pomacea lineata*) as "several metres an hour" (Van Dinther, 1956). Ribi & Arter (1986) documented gender differences in *Viviparus ater* movement rates; 9.4 m/d for males and 4.8 m for females, distances 150 to 300 times their shell lengths.

Based on significant gender-based differences in distances traveled and movement patterns, and increased M:F ratios associated with increased egg production (and no significant effects of environmental factors), we concluded that reproduction is a major driving force for Florida apple snail movements during the breeding season. Michel et al. (2007) concluded that longer distances exhibited by male over female *Lavigeria* snails in a freshwater lake reflected mate searching. Similar gender differences in distances traveled were found for *Viviparous* snails (Ribi & Arter, 1986). Three of six groups of *Viviparous* snails released in a lake exhibited significant directional patterns in their daily movements over ten days; maintaining a bearing was associated with two groups of males in two different sites, but in a third site a Raleigh test indicated significant directionality for a group of females.

Takeichi et al. (2007) found that *P. canaliculata* males were drawn to water-borne female chemicals in the absence of slime trails in a laboratory study, but no such effect was indicated in our field study. We concluded that increased M:F ratios associated with reproductive activity reflected males tracking females that had crawled into traps. Male tracking of females via slime trails deposited during locomotion has been described for *Pomacea canaliculata* (Takeichi et al., 2007), as well as other aquatic species (Erlandsson & Kostylev, 1995). Hanning (1979) described males seeking out females, but did not study slime-trail tracking explicitly. Tracker snails have been shown to move at faster rates than marker snails (those being followed) (Erlandsson & Kostylev, 1995), and this may explain the greater distances traveled by male snails during peak breeding. For Florida apple snail males to track females over long distances, the mucous trail would presumably need to remain intact from one to several days, as has been found for other aquatic snails (Davies & Williams, 1995; Hutchinson et al., 2007).

Gender differences in movement may reflect investment-based reproductive strategies to maximize fitness. Ribi & Arter (1986) described male snails as investing more (relative to females) in movements because they benefit more from increasing potential mate encounters. In contrast, females require fewer matings to achieve maximum fitness potential (which may be constrained by the ability to produce eggs) and consequently move less. Hanning (1979) described incidences of female *P. paludosa* snails being unreceptive to mating, and actively dislodging males attempting to mate. Similar observations have been made for *P. canaliculata* (Burela & Martin, 2009). Each of these observations in *Pomacea* was consistent with the idea that females gain less from additional matings. In a case of a conditional strategy, Tomiyama (1992) concluded that longer more linear movements by young adult sperm-producing land snails (*Achatina fulica*) reflected the need to find egg-producing mates. Older *A. fulica* produce both sperm and eggs, lessening the need for investing in mate finding, so they traveled shorter distances (Tomiyama, 1992).

Movements by Florida apple snails were influenced by gender and reproductive status during their reproductive season. Their ability to routinely move 10–20 m per week and track mates over long distances may be critical for a species that tends to occur at relatively low densities (often < 0.2 snails/m^2), compared to other freshwater gastropods that often occur at dozens or hundreds of individuals per m^2 (Strzelec & Krolczyk, 2004; Jakubik, 2007;

Clark et al., 2008). Additional studies would be required to determine whether trail-following is the mechanism behind the gender differences in movements and changes in M:F ratios found in passive traps that we observed.

ACKNOWLEDGEMENTS

The field project was funded by the South Florida Water Management District (West Palm Beach, Florida) and the St. Johns River Water Management District (Palatka, Florida) through a contract with the Florida Cooperative Fish and Wildlife Research Unit (Gainesville, Florida). Research support was also provided to PCD by the Department of Biology and College of Arts and Sciences at the University of West Florida (Pensacola, Florida). Bethany Wight (UWF) provided valuable assistance in manuscript preparation. We thank Ikuko Fujisaki (University of Florida) for help with statistical analyses. We thank Chris Cattau (UF), Charles D'Asaro (UWF), and three anonymous reviewers for helpful comments on drafts of this manuscript.

LITERATURE CITED

ALBRECHT, E. A., N. B. CARRENO & A. CASTRO-VAZQUEZ, 1996, A quantitative study of the copulation and spawning in the South American apple-snail, *Pomacea canaliculata* (Prosobranchia: Ampullariidae). *The Veliger*, 39: 142–147.

ALDRIDGE, D. W., 1983, Physiological ecology of freshwater prosobranchs. Pp. 330–358, in: W. D. Russel-Hunter, ed., *The Mollusca: Volume 6, Ecology*. Academic Press, New York, 358 pp.

ANDREWS, E. B., 1964, The functional anatomy and histology of the reproductive system of some pilid gastropod molluscs. *Proceedings of the Malacological Society of London*, 36: 121–139.

BURELA, S. & P. R. MARTIN, 2009, Sequential patterns in the mating behavior of the apple snail *Pomacea canaliculata* (Caenogastropoda: Ampullariidae). *Malacologia*, 51: 157–164.

BURKY, K. A. & J. A. BURKY, 1977, Buoyancy changes as related to respiratory behavior in an amphibious snail, *Pomacea urceus* (Muller), from Venezuela. *Nautilus*, 91: 97–104.

CLARK, W. R., C. J. HENRY & C. L. DETTMAN, 2008, Demographic processes influencing population viability of the Iowa Pleistocene snail (*Discus macclintocki*). *American Midland Naturalist*, 160: 129–139.

COFFIN, M. R. S., D. DROLET, D. J. HAMILTON & M. A. BARBEAU, 2008, Effect of immersion at low tide on distribution and movement of the mud snail, *Ilyanassa obsolete* (Say), in the upper Bay of Fundy, eastern Canada. *Journal of Experimental Marine Biology & Ecology*, 364: 110–115.

COWIE, R. H., 2002, Apple snails as agricultural pests: their biology, impact and management. Pp. 145–192, in: G. M. Barker, ed., *Mollusca as crop pests*. CAB International, Wallingford, 576 pp.

CROLL, R. P., 1983, Gastropod chemoreception. *Biological Review*, 58: 293–319.

CROWDER, M. J. & D. J. HAND, 1990, *Analysis of Repeated Measures*. Chapman and Hall, New York, 257 pp.

DARBY, P., 1999, Radio transmitter retrieval in wetlands using a magnetic probe. *Journal of Field Ornithology*, 70: 587–590.

DARBY, P. C., R. E. BENNETTS, J. D. CROOP, P. L. VALENTINE-DARBY & W. M. KITCHENS, 1999, A comparison of sampling techniques for quantifying abundance of the Florida apple snail (*Pomacea paludosa* Say). *Journal of Molluscan Studies*, 65: 195–208.

DARBY, P. C., R. E. BENNETTS & L. B. KARUNARATNE, 2006, Apple snail densities in habitats used by foraging snail kites. *Florida Field Naturalist*, 34: 37–47.

DARBY, P. C., R. E. BENNETTS, S. J. MILLER & H. F. PERCIVAL, 2002, Movements of Florida apple snails in relation to water levels and drying events. *Wetlands*, 22: 489–498.

DARBY, P. C., BENNETTS, R. E. & H. F. PERCIVAL, 2008, Dry down impacts on apple snail demography: implications for wetlands water management. *Wetlands*, 28: 204–214.

DARBY, P. C., P. L. VALENTINE-DARBY, H. F. PERCIVAL & W. M. KITCHENS, 2001, Collecting Florida apple snails (*Pomacea paludosa*) from wetland habitats using funnel traps. *Wetlands*, 21: 308–311.

DARBY, P. C., P. L. VALENTINE-DARBY & H. F. PERCIVAL, 2003, Dry season survival in a Florida apple snail (*Pomacea paludosa* Say) population. *Malacologia*, 45: 179–184.

DAVIES, M. S. & G. A. WILLIAMS, 1995, Pedal mucus of a tropical limpet, *Cellana grata* (Gould): energetics, production and fate. *Journal of Experimental Marine Biology & Ecology*, 186: 77–87.

DICKEY B. F. & T. M. McCARTHY, 2007, Predator-prey interactions between crayfish (*Orconectes juvenilis*) and snails (*Physa gyrina*) are affected by spatial scale and chemical cues. *Invertebrate Biology*, 126(1): 57–66.

DINTER, I., 1974, Pheromonal behaviour in the marine snail *Littorina littorea* (Linnaeus). *The Veliger*, 17: 37–39.

ERLANDSSON, J. & V. KOSTYLEV, 1995, Trail following, speed and fractal dimension of movement in a marine prosobranch, *Littorina littorea*, during a mating and a non-mating season. *Marine Biology*, 122: 87–94.

HANNING, G. W., 1979, Aspects of reproduction in *Pomacea paludosa* (Mesogastropoda: Pilidae). MS Thesis, Florida State University, Tallahassee, 138 pp.

HOFFMAN, A. L., J. D. OLDEN, J. B. MONROE, N. L. POFF, T. WELLNITZ & J. A. WIENS, 2006, Current velocity and habitat patchiness shape stream herbivore movement. *Oikos*, 115: 358–368.

HURDLE, M.T., 1974, Life history studies and habitat requirements of the apple snail at Lake Woodruff National Wildlife Refuge. *Proceedings of the 27th Annual Conference of the Southeastern Association of Game and Fish Commissioners*, 27: 215–224.

HUTCHINSON, N., M. S. DAVIES, J. S. S. NG & G. A. WILLIAMS, 2007, Trail following behaviour in relation to pedal mucus production in the intertidal gastropod *Monodonta labio* (Linnaeus). *Journal of Experimental Marine Biology & Ecology*, 349: 313–322.

JAMMALAMADAKA, S. R. & A. SENGUPTA, 2001, *Topics in circular statistics*. World Scientific, Singapore, 322 pp.

JAKUBIK, B., 2007, Egg number-female body weight relationship in fresh water snail (*Viviparus viviparus* L.) population in a reservoir. *Polish Journal of Ecology*, 55: 325–336.

LOUDA, S. M. & K. R. McKAYE, 1982, Diurnal movements in populations of the prosobranch *Lanistes nyassanus* at Cape Maclear, Lake Malawi, Africa. *Malacologia*, 23: 13–21.

LOWE, E. F., 1983, *Distribution and structure of floodplain plant communities in the upper basin of the St. Johns River, Florida*. St. Johns River Water Management District Technical Publication, Palatka, Florida, 50 pp.

MARDIA, K. V., 1972, *Statistics of directional data*. Academic Press, London, UK, 357 pp.

McCULLAGH, P. & J. A. NELDER, 1989, *Generalized Linear Models*. Chapman and Hall, London, 511 pp.

MICHEL, E., P. B. MCINTYRE & J. CHAN, 2007, A snail's space sets a snail's pace: movement rates of *Lavigeria* gastropods in Lake Tanganyika, East Africa. *Journal of Molluscan Studies*, 73: 195–198.

PARDO, L. M. & L. E. JOHNSON, 2004, Activity and shelter use of an intertidal snail: effects of sex, reproductive condition and tidal cycle. *Journal of Experimental Marine Biology & Ecology*, 301: 175–191.

PENNACK, R. W., 2001, *Fresh-water invertebrates of the United States: Protozoa to Mollusca,* 4th ed. John Wiley & Sons, New York, 648 pp.

RIBI, G. & H. ARTER, 1986, Sex related difference of movement speed in the freshwater snail *Viviparus ater*. *Journal of Molluscan Studies*, 52: 91–96.

SAS, 1992, *Technical Report P-229 SAS/STAT Software: changes and enhancements.* SAS Institute Incorporated, Raleigh, North Carolina, 1,162 pp.

SEARLE, S. R., G. CASSELLA & C. E. MCCULLOCH, 1992, *Variance Components*. John Wiley and Sons, New York, 501 pp.

SHAHEEN, N., K. PATEL, P. PATEL, M. MOORE & M. A. HARRINGTON, 2005, A predatory snail distinguishes between conspecific and heterospecific snails and trails based on chemical cues in slime. *Animal Behaviour*, 70: 1067–1077.

SNIDER, S. B. & J. F. GILLIAM, 2008, Movement ecology: size-specific behavioral response of an invasive snail to food availability. *Ecology*, 89(7): 1961–1971.

STEVENS, A. S., Z. C. WELCH, P. C. DARBY & H. F. PERCIVAL, 2002, Temperature effects on Florida apple snail activity: implications for snail kite (*Rostrhamus sociabilis)* foraging success and distribution. *Wildlife Society Bulletin*, 30: 76–81.

STRZELEC, M. & A. KROLCZYK, 2004, Factors affecting snail (Gastropoda) community structure in the upper course of the Warta river (Poland). *Biologia Bratislava*, 59: 159–163.

TAKEDA, N. & H. TSURUOKA, 1979, A sex pheromone secreting gland in the terrestrial snail, *Euhadra peliomphala*. *Journal of Experimental Zoology*, 207: 17–26.

TAKEICHI, M., Y. HIRAI & Y. YUSA, 2007, A waterborne sex pheromone and trail following in the apple snail, *Pomacea canaliculata*. *Journal of Molluscan Studies*, 73: 275–278.

THOMPSON, F. G., 1984, *The freshwater snails of Florida: a manual for identification*. University of Florida Press, Gainesville, 94 pp.

TOMIYAMA, K., 1992, Homing behaviour of the giant African snail, *Achatina fulica* (Ferussac) (Gastropoda; Pulmonata). *Journal of Ethology*, 10: 139–147.

TURNER, R. L., 1996, Use of stems of emergent vegetation for oviposition by the Florida apple snail (*Pomacea paludosa*), and implications for marsh management. *Florida Scientist*, 59: 34–49.

VALENTINE-DARBY, P. L., P. C. DARBY, R. E. BENNETTS, W. M. KITCHENS & H. F. PERCIVAL, 2008, The use of mark-recapture to estimate Florida apple snail (*Pomacea paludosa* Say) density in wetland habitats. *Florida Scientist*, 71: 115–127.

VAN DINTHER, J. B. M., 1956, Control of *Pomacea* (*Ampullaria*) snails in rice fields. Agricultural Experiment Station, Paramaribo, *Surinam Bulletin*, 68: 1–20 [as cited in Cowie, 2002].

WELLS, M. J. & S. K. L. BUCKLEY, 1972, Snails and trails. *Animal Behaviour*, 20: 345–355.

YUSA, Y. & Y. SUZUKI, 2002, A snail with unbiased population sex ratios but highly biased brood sex ratios. *Proceedings of the Royal Society of London B*, 270: 283–288.

Revised ms. accepted 5 February 2011